GLANDULAR STRUCTURE OF THE ABDOMINAL APPENDAGES OF A TERMITE GUEST (Spirachtha)*

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(Figure 41, Plates XVI-XVII)

Introduction.

Some of the specimens of *Spirachtha,* collected by Mr. Alfred Emerson of the University of Pittsburgh in nests of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren) in British Guiana, were given to me to determine whether or not the abdominal appendages are glandular.

Emerson informs me by correspondence that his specimens of *Spirachtha* were identified by Dr. W. M. Mann of the Bureau of Entomology as two new species—*S. schiödtei* and *mirabilis* Mann. The material sectioned by me belongs to the latter species, but Emerson made his observations on both species; however, he says: "As far as I observed, the habits of both of the *Spirachtha* were exactly the same, and both species came from the same nests."

The live insects were fixed by Emerson in hot corrosive sublimate plus a little acetic acid and then allowed to cool, and finally were preserved in 85 per cent alcohol. Parts of the abdominal appendages and the abdomen with the appendages intact were embedded in 60° parraffin. Sections were cut five microns in thickness and were stained in Ehrlich's hematoxylin and eosin. The drawings, except fig. 41, are original and were made at the base of the microscope with the aid of a camera lucida. Figure 41 was made by Emerson from a specimen, but I have added a few hairs and some shading to it.

The following references are all that I can find which relate directly to the abdominal appendages of *Spirachtha.*

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Schiödte (1853) says: "The abdomen is furnished with three pairs of appendages, which are elongate, cylindrical, 2-jointed, membraneous, and moveable by muscles at the base. The appendages are perhaps intended for the same purpose as the tufts of hairs on the abdomen of the genus *Claviger*, which are known to be sucked by the ants." The same author (1856, p. 181), after having prepared sections from specimens preserved

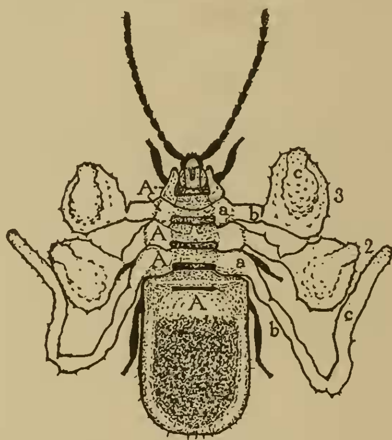

FIG. 41. *SPIRACHTHA MIRABILIS* MANN

Dorsal view showing abdominal appendages (1, 2 and 3), which consist of portions **a**, **b** and **c**; only the last two being glandular. Those portions marked A are the abdomen which conceals all the thorax and head, except parts of the legs, the antennae and anterior part of the head (all in solid black). Greatly enlarged. Photographed and originally drawn by Emerson, but later slightly modified by the writer.

in alcohol, was not able to decide definitely whether or not these appendages are glandular in structure. He says that there is a pair of muscles at the base of these organs, and consequently they are moveable. They are formed from prolongations of the abdominal integument, and have thick walls. Their structure appears to be homogeneous, and their contents is composed of clear granules of an irregular and globular form.

External Structure of Abdominal Appendages.

This staphylinid beetle, about the size of a common pin head, is most remarkable in that the abdomen bends forward so that the latter lies directly over the thorax and head. Further than this, the abdomen (Fig. 41*A*) bears three pairs of appendages (*1*, *2* and *3*), the size and shape of which vary considerably in different specimens. Very few of the specimens, however, have perfectly developed appendages. Emerson says that the appendages were of various sizes or were in various stages of development when observed in the field; some possessed only small knobs on the abdomen, while in a few the appendages were well developed as shown in Fig. 41.

The first pair of appendages (Fig. 41, *1*) is unusually long and filamentous, while the second and third pairs are elongate or club shaped, but when perfectly developed their distal ends (*2* and *3*) are more or less globular in shape, as represented in Fig. 41. The appendages, when fixed in the corrosive sublimate solution, are white, soft and fleshy-like structures, and are easily sectioned. Emerson says that when the insects are alive, the appendages are held up over the abdomen; sometimes those of one side touching those of the other side. The first pair, arising from the fourth abdominal segment, is held up in the air, each resembling the letter S. The second and third pairs, arising from the fifth and sixth abdominal segments, were observed to be slightly moveable through a vertical plane at right angles to the body. Emerson observed that when the appendages were moved, all of them moved at the same instant. He thinks that both sexes develop these extraordinary appendages and that they are postimaginal structures.

Internal Structure of Abdominal Appendages.

Each appendage arises from a fleshy prolongation (Fig. 41, *a*) of the abdomen, and appears to be 2-segmented, but sections show that the articulations between portions marked a and **b** and between **b** and **c** are nothing more than constrictions with thinner cuticula than elsewhere. The constriction between a and **b** is shallow, while the one between b and c is deep. Several muscle fibers run diagonally across the portion marked **a**, but only a few other fibers unite with the integument in the constriction, and no muscles were seen in the apparent segments **b** and **c**. Judging from this arrangement, the appendages certainly cannot be moved very much.

A microscopical examination of the integuments (not treated with KOH) of these appendages did not show any pores and only two types of hairs. The cuticula is literally covered with tiny prickles or pseudohairs and (Plate XVI, 5, Hr^1) many comparatively large hairs (Plates XVI-XVII, 5, 14, Hr) were observed arising singly from miniature mounds, widely scattered.

Sections through the portions marked b and c (Fig. 41) reveal the most peculiar arrangement of tissues that I have ever observed. These portions (Plates XVI-XVII, 12-14) appear hollow, but are really filled with a coagulated liquid, apparently blood (Plate XVII, 14, Bl.). The walls are thick and consist of four layers; the two outermost ones being the cuticula (Plate XVII, E, D), the middle one the hypodermis (Hyp), and the innermost one the basement membrane (M) of the hypodermis. Passing through the hypodermis from the basement membrane to the outer layer of the cuticula there are many dark strands; some of these (S) are attached to the bases of the hairs (Hr), and the others (St) either to the cuticula directly or at the bases of tiny pores (P). These various structures are colored very beautifully in sections passed through alcohol containing iodine, and stained by Ehrlich's hematoxylin and eosin. The blood and basement membrane are colored pinkish by the eosin, but the later takes the deeper color; the hypodermis is stained purple by the hematoxylin; the inner layer of the cuticula (D) and the strands are stained brownish by the iodine; and the outer layer of the cuticula (E) remains unstained, being whitish or semi-transparent.

A more careful study of these various structures shows the following details. The outer and inner layers of the cuticula are practically equal in thickness. The former contains numerous tiny pores (Plate XVI, 11, P) whose outer ends are funnel-shaped, while the inner ends are straight or curved. The pores are practically all single openings, but one double pore (17) was found. These pores are peculiar in that the outer cuticula surrounding them is considerably thicker than elsewhere, thus making semispherical projections which extend into the inner cuticula.

While there is nothing uncommon about the outer cuticula, except its pores, the inner cuticula is very peculiarly modified. The latter usually appears porous or spongy (Plate XVI, 4, 6, 8, D), but may be stratified (5, 11), or may occasionally be

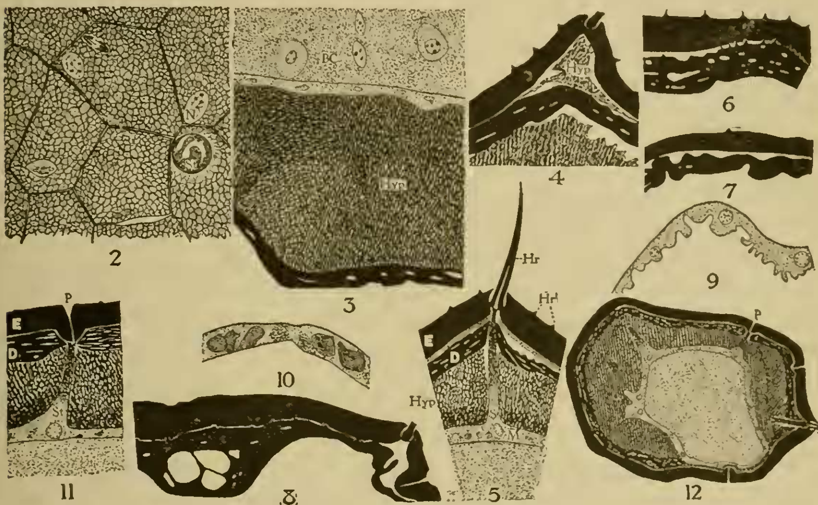

Plate XVI. *S. MIRABILIS* MANN

Internal structure of abdominal appendages.

2, end view of columnar hypodermal cells, showing nucleus (N) and stands (S and St) in cross section; 3, longitudinal view of glandular hypodermal cells (Hyp) and blood cells (BC); 4, 5 and 11, wall of appendage, showing original hypodermis (Hyp^1), hair (Hr), tiny prickles (Hr^1), outer cuticula (E), inner cuticula (D), pore (P), glandular hypodermis (Hyp), basement membrane (M), and strands (S and St) in longitudinal view; 6 to 8, various types of the dermis; 9 and 10, two types of the basement membrane; 12, cross section (semidiagrammatic) of the smaller bulb-shaped end of an appendage, showing all of the internal structures; 2 to 11, X 505, and 12, X 105.

wavy (7). It lies against the outer cuticula and is firmly anchored there by many tiny prickle-like projections (6, 8), extending into the outer layer. In order to distinguish the inner from the outer cuticula in the various drawings, a white space has been left between these two layers.

Section passing crosswise through the hypodermal cells show that these are usually five or six sided columnar cells (Plate XVI, 2), whose cut ends appear net-like and resemble plant cells more than animal cells. Their nuclei (N) are scarcely discernible and only appear as faint elliptical areas which contain a few dark particles with a few radiating lines. It is strange that these nuclei should be so inconspicuous, because ordinarily nuclei are the most conspicuous parts of cells. Perhaps the fixation was not good for these nuclei.

Sections passing lengthwise through the hypodermal cells usually indicate that the hypodermis consists of more than one layer of cells, but upon closer examination it becomes evident that the hypodermis really consists of only one layer (Plate XVI, 3). In longitudinal sections the contents of the cells appear to consist of coagulated streaks, somewhat resembling strings of beads, which generally extend lengthwise through the cell, but sometimes diagonally across it. The longitudinal walls of the cells are conspicuous as dark lines, usually running in zigzag style, while in cross sections the walls appear as curved or straight lines. Under a high magnification each dark line appears double as shown in (2, 3).

Like the inner cuticula and hypodermis, the basement membrane is also unusually developed. So far as I am aware, the basement membrane in sections of insects almost always appears as a single line without nuclei, but in spiders (McIndoo, 1911) it appears as a double line with nuclei. This may be due to the fact that the hypodermis in spiders is always thick, never becomes atrophied, but continues to function as long as the spider lives. This explanation may possibly serve to explain why the basement membrane in these abdominal appendages is so highly developed; here both walls are always discernible (Plate XVI, 5, 9-11), and nuclei are usually seen between them. The inner wall is generally more or less smooth, but occasionally it is very rough and may bear finger-shaped or papilla-like projections (9), which extend into the blood.

For some time the dark strands, already mentioned, were a puzzle to me, but now I believe that I can satisfactorily explain them. They are very conspicuous in all the sections made, and appear in four different conditions; fragments may be seen adhering to the cuticula or bases of the hairs; small isolated portions (Plate XVI, 2, 12, S), may be observed in either cross or longitudinal sections of the hypodermal cells; prolongations (12) of various length may be seen extending from the basement membrane into the hypodermis; and occasionally a complete strand (5, S and 11, St) may be observed. Their outer end (2, S and St) appear to be spongy and in structure are similar to the inner cuticula, but their inner ends seem to be as soft as the basement membrane. Practically every hair has a strand attached to its base, while only about one half of the pores have strands attached at their inner ends. Those strands running to the hairs look darker in sections and are much narrower than are the other ones described. The probable function of these strands is stated under "Interpretation of Results."

In life these abdominal appendages are probably completely filled with blood, because in sections the coagulated remains of the blood almost fill the entire cavity. Two types of blood cells (Plate XVI. 3, BC) were found in the blood. The smaller type, although probably not blood cells at all, is the commoner.

Interpretation of Results.

After a preliminary examination of the sections prepared, my first interpretation of these appendages was that the liquid found in them is a secretion which finds its way to the exterior through the strands and pores. This interpretation was found to be incorrect for the three following reasons: 1 The quantity of liquid contained in all six appendages is more than that of the blood contained in the remainder of the abdomen; thus, the source of any secretion must always be greater than the secretion itself. 2 This liquid contains blood cells, appears the same in structure, and has the same color as the blood found elsewhere. And 3, if the strands were efferent tubes they should be hollow in order to permit the secretion to pass freely to the exterior.

My interpretation now is that the blood passes freely through the basement membrane and inner ends of the strands into the hypodermal cells which act as secreting or gland cells.

If this is true the secretion then passes from the hypodermis into the outer ends of the strands and into the inner cuticula which serves as a reservoir to store the secretion. From this reservoir the secretion passes through the numerous tiny pores to the exterior where it probably spreads over the entire surface of the appendages and abdomen. This view is supported by the following facts. Emerson says that the termites carry these beetles about from place to place and that he often saw them lick not only the abdominal appendages but also the entire bodies of these insects. The inner ends of the hypodermal cells must be extremely active, judging from their deeper staining capacity. The basement membrane and inner ends of the strands contain coagulated particles like those in the blood, thus indicating that the blood passes freely into the hypodermis. The secretion must be different from the blood, because no remains of it can be found in the sections prepared. It may be of an oily or fatty nature and evidently totally soluble in the reagents used.

It would be interesting to know the exact sequence of formation of the various structures in the walls of these appendages. The formation is perhaps about as follows: The original hypodermis (Plate XVI, 4, 5, Hyp^1), little of which remains, first secretes the outer cuticula and hairs, then the inner cuticula; afterwards instead of its becoming atrophied as usual, it becomes greatly hypertrophied and secretes an entirely different substance which probably serves a nutritive purpose. Since the hypodermis is a thick, soft and flabby membrane it needs supports and a means of firmly anchoring it to the dermis. All of this is accomplished by the semirigid strands. Those strands attached to the hairs might originally have been trichogen cells, but now they are entirely different and certainly have a different function. In fact it seems that all the strands have originated as outgrowths from the basement membrane, because they are still attached to it and a large nucleus is usually present in this membrane where a strand departs The strands are attached to the bases of hairs and pores, because these projections serve as good places for attaching them.

The various structures, as described, are present in all parts of the appendages marked **b** and **c** (Fig. 41), but the blood chamber is not always centrally located. Sometimes, as in the smaller bulb-shaped end of an appendage, the blood chamber (Plate XVI, 12) has shifted to one side, totally eliminating the hypodermis from that side. In the portion marked a (Fig. 41) and in the remainder of the abdomen none

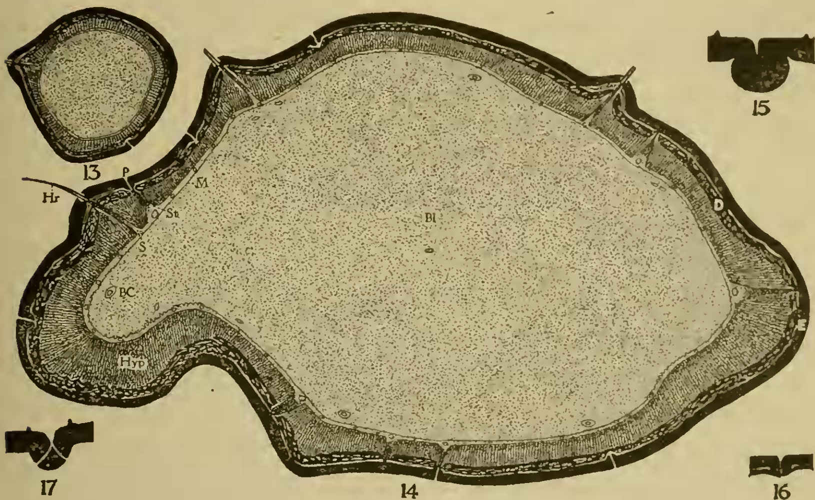

Plate XVII. *S. MIRABILIS* MANN.
Internal structure of abdominal appendages.

13, cross section through portion b (Fig. 41) of first appendage; 14, oblique section through portion c of second or third appendage, showing following internal structures: pore (P), outer cuticula (E), inner cuticula (D), glandular hypodermis (Hyp.), strands (S and St), basement membrane (M), blood cells (BC), and blood (Bl); both diagrammatic, and both X 105; 15 and 17, various sizes and types of pores, X 505; 15 to 17, sections similiar to 14; 16, from abdomen; 15, largest pore; 16, smallest pore found.

of these structures are unusually developed and only traces of some of them can be found. Starting with the proximal end of portion **b** and following the sections into the abdomen, it is seen that the highly developed hypodermis with its basement membrane suddenly disappears and that the inner and outer cuticula gradually become thinner so that in the portion a all that remains is: 1 a thinner outer cuticula with an occasional pore; 2 a very thin inner cuticula, slightly porous; and 3 a trace of the original hypodermis. In the abdomen the outer cuticula is still thinner and only a trace of the inner cuticula and hypodermis can be found. Here an occasional pore (Plate XVII, 16), the smallest of all, is still present but the inner cuticula is no longer porous. In these sections there is nothing unusual about the anatomy of the abdomen. The greater part of the space is filled with the intestine, cut two or three times thus showing that it is much convoluted. At certain places the intestine seems very large and contains many particles, resembling bits of vegetable matter. Other structures, apparently eggs in their follicles are present; besides muscles, blood and the fat cells. The fat body is comparatively small and seldom lies against the cuticula.

General Discussion.

In referring to the literature on this subject, I find only one insect in which the apparent arrangement of tissues is similar to that already described for *Spirachtha;* yet in this one there is no similarity if these tissues have been correctly named. This staphylinid beetle (*Termitomimus*) was found in considerable numbers by Trägårdh (1907a) in the *Eutermes* colonies of Zululand. Trägårdh says that this genus matches *Spirachtha* with regard to the peculiar development of the abdomen and the mouth-parts. The large abdomen bears no appendages, but curves upward and forward so as to cover completely the thorax and posterior half of the head. For description he has divided the abdomen into a "pseudocaput," a "pseudothorax" and "pseudoabdomen." Sections through the "pseudothoracic" projections show four layers in the thick body wall. He calls the outer and inner layers of the cuticula epiostracum and endostracum respectively. In the position of my glandular hypodermis, he finds a cyanophilous tissue of a spongy appearance which sometimes exhibits a very distinct radial structure, sometimes is concentrically stratified and contains numerous granules which are also to be found in the trichogen cells. He thinks that this tissue is a fluid, which has either passed through the hypodermis and is a derivate from the fat body, or it is a secretion produced by the hypodermis and is coagulated by the method of fixation. It seems to me that this tissue, which is poorly fixed, might correspond to my glandular hypodermis. In the positions of my basement membrane and the strands, running to the hairs, he finds two structures which he calls hypodermis and trichogen cells respectively. He imagines that the secretion passes through the cuticula, although he saw no pores at this place, but at other places in the cuticula near which lie fat cells he saw many extremely fine pores.

Trägårdh found two pairs of glands opening into the cuticular folds at the dorsal side of the neck of *Termitomimus*. He calls them cephalic and prothoracic glands, because the unicellular hypodermal glands of the former lie in the head and those of the latter in the prothorax. Each gland cell opens to the exterior through a tiny pore. He does not think that these glands are in any way connected with the termitophilous life of *Termitomimus*.

While it is exceptionally rare for any adult insect to bear appendages or projections similar to those already described, many larval insects bearing unusual thoracic and abdominal appendages have already been found.

Silvestri (1920) found unusual thoracic and abdominal appendages on certain dipterous and lepidopterous larvae, and also apparently eight pairs of lateral appendages on the coleopterous larva of *Troctontus*, all of which were taken from termite nests in Africa. He seems to have found glands in only the tiny club-shaped appendages of the last named insect. These consist of many very large unicellular, hypodermal glands. They lie in a thick hypodermis and open to the exterior through pores. Silvestri thinks that they secrete a special substance for the termites.

Wheeler (1918) found unusual thoracic and abdominal protuberances or appendages on three species of ant larvae belonging to the genera, *Tetraponera* and *Pachysima*. Speaking of the tubercles of *T. tessmanni*, Wheeler (p. 306) says:

"Sections and stained, cleared preparations of the whole larva show that the various tubercles contain portions of the fat body, at least in the bases of their cavities, and next to the hypodermis a dense, granular substance, evidently a coagulated liquid produced by the underlying adiphocytes, or trophocytes. . . . Around the bases of tubercles are muscles so arranged that their contraction must increase the pressure on the fat and granular liquid and in all probability cause the later to exude through the hypodermis and delicate chitinous cuticle onto the surface. The whole arrangement of the tubercles, in fact, constitutes a system of exudate organs, or exudatoria, as I shall call them, adapted to secrete substances that can be licked up by the ants when they are feeding and caring for the larvae."

Wheeler also studied sections through the appendages of *P. latifrons* and found a similar arrangement of tissues, but in the fat cells in these sections he imagined that he saw urate crystals, which caused him to believe that these cells function as a storage kidney till the malpighian vessels are sufficiently developed to excrete. To me Wheeler has not shown any evidence that these appendages are really exudatory, but it is very probable that they are. He saw no pores in the cuticula and does not say how his coagulated liquid differs from the blood, but in support of his view he claims that we must interpret the exudatoria as very primitive glands, which in all probability have arisen as new formations and not as homologues of the embryonic legs. He (p. 313) says:

"They are, as we have seen, small diverticula like the embryonic legs, consisting of hypodermis and its overlying cuticula and containing a portion of the fat-body separated from the hypodermis by a granular liquid. Now the fat-body of the insects may be regarded as a diffuse ductless gland, the cells (trophocytes) of which take certain substances from the blood in which they lie, store them in the cytoplasm as fat-globules or proteid granules and later return them to the blood in a more finely divided, if not chemically modified form. The exudate which accumulates in the distal ends of the exudatoria is therefore merely blood charged with nutrient substances from the fat-cells, and either filters gradually through the hypodermis and overlying cuticle or is forced through them by muscular pressure. At first sight it would seem that the cuticle must be impervious to such a liquid, but a consideration of the more recent work on the minute structure of chitin * * * shows that there is nothing to prevent the passage of a thin fatty liquid, even if it were not under pressure and even if the cuticle were much thicker than it is in the ant larva. The cuticle is a colloid, either of a reticular structure, as Kapzow believes, or formed of horizontal layers of very fine fibrillæ crossing one another at an angle of 60° as most investigators, including Biedermann and Casper, maintain. Between the fibrillæ are regularly distributed and extremely fine openings or 'pore canals,' through which a liquid might readily pass as if the cuticle were a filter."

In further support of his view, Wheeler cites the work done on certain meloid, cantharid, lampyrid, coccinellid and chrysomelid beetles in which a liquid, usually regarded as blood plasma charged with cantharidin, is discharged from the articulations of their legs. Wheeler has overlooked my work (1916) in which I found gland pores in the femoro-tibial articulations of meloid and coccinellid beetles, and in *Epilachna borealis* I described two types of gland cells which discharge the liquid through these pores. It is also possible that the other named insects have glands which discharge secretions from their legs.

Wasmann (1903), Trägårdh (1907 *a* and *b*) and Holmgren (1909) have published much concerning the exudate organs of myrmecophiles and termitophiles, but considerable of the work done on the finer anatomy is not clear to me, although Wheeler uses their results to support his view.

Wheeler (1910, p. 399) states that students of myrmecophily observed that true guests of ants generally bear tufts of hairs or trichomes which are assiduously licked by the ants, and Wasmann (1903), who has written much about these structures, shows that the trichomes are borne by the integument at points or depressions where clusters of unicellular glands open, and that they function by rapidly diffusing some aromatic secretion. Wasmann thinks that the secretion is not liquid, but perhaps a fatty ether, thus being volatile or etherial. The ants are so fond of it that he thinks it must affect them very much as a good cigar affects a smoker. Wheeler adds: "Perhaps it would be nearer the truth to say that its fascination is more like that of catnip or oil of bergamot on the various members of the cat family."

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